

On the Biology and Systematic Position of *Microtus abbreviatus* Miller, a Vole endemic to the St. Matthew Islands, Bering Sea

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During a five-week period in 1954 (2 August — 6 September), we undertook a biological reconnaissance of St. Matthew Island, the largest of the St. Matthew group. Although we made general collections of the flora and fauna, our main effort was directed to the study of the endemic vole, *Microtus abbreviatus* Miller, 1899, which was present in large numbers at the time. In addition to 238 animals examined on the island, we brought 12 alive to the laboratory, where a breeding colony was established.

The purpose of this paper is to report general observations on St. Matthew Island, to describe some of the biological characteristics of *M. abbreviatus* as determined from both wild and captive animals, and to discuss the systematic status of this vole.

Our data have been supplemented by records and specimens made available by Dr. F. H. FAY, of this Laboratory, who spent 18 days on St. Matthew Island during July and August, 1963. Mr. R. J. HENSEL, U. S. Fish and Wildlife Service, Kodiak, permitted us to abstract information from the unpublished notes of Mr. F. L. BEALS, who recorded biological observations on St. Matthew Island from 30 June to 16 August 1944.

The St. Matthew Islands

Historical Survey

The St. Matthew Islands were discovered by Lieutenant SYND of the Russian Navy in the course of explorations during the years 1764–1768 (COXE, 1803, p. 264). A chart of SYND's voyage, reproduced by COXE, show "I. Apost. Matthei" lying to the southwest of their actual position. COOK (1822, p. 657) reached the islands on 29 July 1778 and believed himself to be their discoverer.

The Billings Expedition next visited the islands, on 14 July 1791, when a landing was made and some biological observations recorded (SAUER, 1802). Some twenty years later (in 1810, according to DALL, 1870), a group of Russians and Aleuts settled briefly on St. Matthew Island in order to hunt polar bears. Probably it was they to whom VON CHAMISSE (p. 294, in VON KOTZEBUE, 1821) referred when he stated that, of the several people who proposed to overwinter, only three survived by spring. From this time until the end of the century, biological information was obtained by several expeditions. During September, 1827, Captain LÜTKE and his company on the ship SENIAVIN spent seven days attempting to survey the islands. The observations recorded by VON KITTLITZ (1858, p. 300) were part of the results of this effort. While visiting the "seal islands" in the Bering Sea, H. W. ELLIOTT and W. MAYNARD landed on St. Matthew Island on 5 August 1874, and both reported briefly on the flora and fauna (MAYNARD, 1876; ELLIOTT, 1882). Some collections were made by C. H. TOWNSEND when the revenue cutter CORWIN stopped at Hall Island on 8 September 1885, and his findings were included in the report of the cruise (TOWNSEND, in HEALY, 1887, p. 96). In 1891, while a member of the International Fur Seal Commission, G. M. DAWSON

(1894) studied geological features of the islands. Members of the Harriman Alaska Expedition collected plants and animals there on 14–15 July 1899.

More recently, data on the birds and mammals were reported by G. D. HANNA (1917, 1920), who spent from 7 to 13 July 1916 on the islands: HANNA (1920, p. 121) stated that two trappers had passed the winter of 1912–1913 on St. Matthew Island. The remains of their cabins and equipment were found in 1944 by F. L. BEALS (unpublished notes), who spent almost seven weeks (30 June–16 August) making biological observations just prior to the introduction of reindeer there by the U. S. Coast Guard. St. Matthew Island was occupied by United States' military forces during 1942–1944. Some years later, a study of the reindeer was begun by KLEIN (1959), whose report includes detailed information on the vegetation and indigenous mammals and birds.

Geographic Features

Of volcanic origin, the St. Matthew Islands lie in the Bering Sea at lat. $60^{\circ}30'$ N. by long. 173° W. (approx.), in waters about 54 to 66 m deep. Pinnacle Island, about 2.5 km long, rises precipitously from the sea to an altitude of some 370 m. Situated

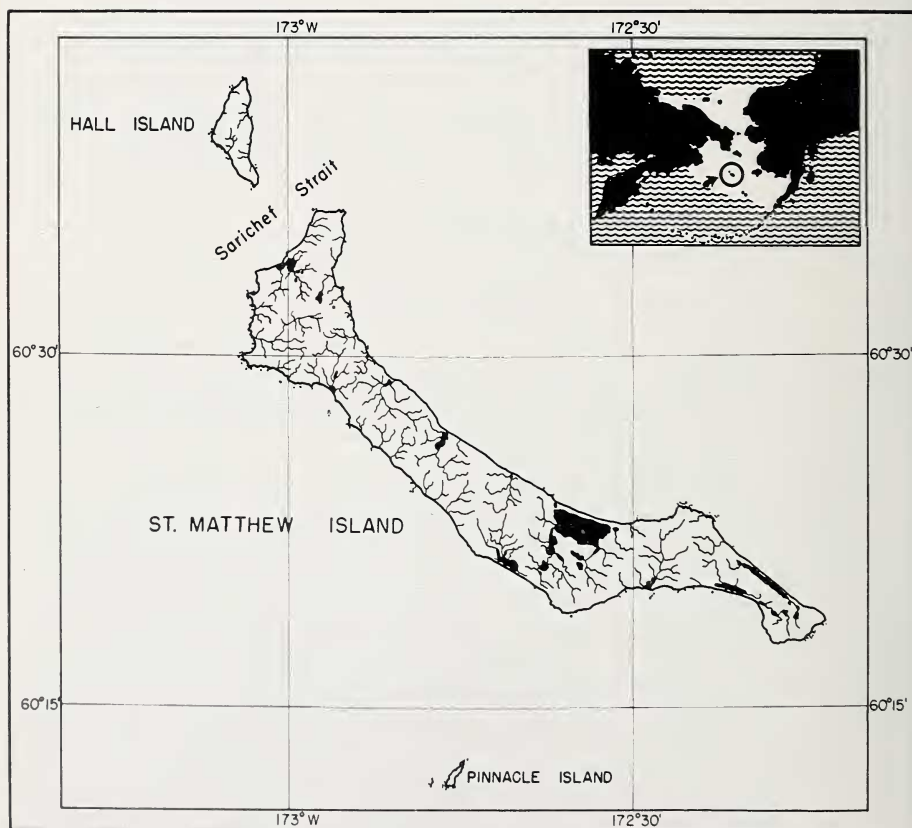


Fig. 1. Map of the St. Matthew Islands. In the inset is shown the relationship of the islands (arrow) to the Asian and North American land masses; the unshaded area represents the limits of the Bering-Chukchi platform.

farthest to the northwest, Hall Island, about 9 km in greatest length and up to 507 m in altitude, is surrounded by steep cliffs.

St. Matthew Island, the largest of the three, is about 52 km (32.5 miles long, 2 to 9.5 km wide, and northwesterly-southeasterly in orientation (Fig. 1). The series of eroded, smoothly contoured mountain ridges extending across the island in a north-south direction range in height up to 459 m. Throughout the length of the island, most of these transecting ridges abut against the sea in cliffs, the formation of which has come about largely through the action of the sea. Extensive lowlands exist in the southeastern half of the island; these as well as some of the steep valleys extending to sea level are bordered by gravel or boulder beaches. Several lakes, some brackish, have been impounded by gravel dikes formed by the sea. The largest lake, having a chloride content of about 20 ppm in 1954, is about 4.8 km long by about 2 km wide. Fresh-water ponds, not all permanent, and smaller lakes are numerous. The small streams are often narrow and deep. Some empty into the sea through gravel barriers. Driftwood in a broad zone has accumulated along the low beach separating the largest lake from the sea on the northern shore.

Climate

Moderately low temperatures, high winds, and frequent fog and rain in summer characterize the climate of the islands. Data on the weather of St. Matthew Island for the period October, 1942,

to September, 1944, were kindly provided by the Regional Climatologist, U. S. Weather Bureau, Anchorage. Although incomplete, these data (Table 1) provide an indication of ranges in temperature and monthly precipitation. During August–September, 1954, we recorded fog and/or rain on 27 days of the 36. Three days were clear, and six partially clear. Temperatures from 7° to 14° C. were recorded, but a range from 9° to 12° C. was usual.

That the islands are free of pack ice from about June to November has been indicated. However, since they lie near the southern limit to which the sea ice extends, the length of the ice-free time can be expected to vary from year to year.

Table 1

Some climatic data for St. Matthew Island

October, 1942 — September, 1944

Year	Month	Precipitation (mm)	Wind: Prevailing Direction	Temperature (° C)	
				Max.	Min.
1942	October	32.7	NW	3.0	– 0.2
	November	—	N	– 0.6	– 4.0
	December	—	NE	– 10.5	– 14.2
1943	January	—	NNE	– 10.1	– 14.7
	February	—	NNE	– 11.8	– 17.2
	March	—	N	– 4.8	– 9.3
	April	—	NE	– 3.5	– 7.8
	May	—	NNE	2.8	– 0.9
	June	—	SW	8.1	2.5
	July	—	SW	10.1	5.3
	August	—	SW	10.3	6.8
	September	52.8	NNE	7.5	2.8
	October	45.9	NNE	4.0	0.2
	November	35.5	NNE	0.3	– 3.0
1944	December	20.8	N	– 6.3	– 11.0
	January	21.3	NE	– 10.8	– 17.2
	February	37.0	NNE	– 6.0	– 12.1
	March	8.1	NNE	– 9.2	– 13.8
	April	13.2	NNE	– 4.1	– 11.1
	May	20.8	NNE	1.8	– 2.5
	June	22.6	NNE	5.1	0.5
	July	37.3	NNE	8.7	4.1
	August	73.4	W	9.4	6.0
	September	17.5	WNW	8.2	4.0

Vegetation

In general, those species of plants present extensively in the North Pacific region comprise the flora of St. Matthew Island. The plant growth is less luxuriant than that on the Pribilof Islands and more closely resembles that of St. Lawrence Island, to the north. The vegetation is low, and all of the woody plants are prostrate.

On lichens, mosses, and some other groups, reports were published in the volumes of the Harriman Alaska Expedition. Records of flowering plants from the St. Matthew Islands have been compiled by HULTÉN (1941–1950). A list of species collected during July–August, 1957, has been given by KLEIN (1959), who also discussed the effects of the introduced reindeer on the vegetation. Our collections in 1954 included over a hundred species of higher plants, 18 species of the more prominent bryophytes, and 16 species of lichens. No doubt we overlooked some of the early-flowering vascular plants.

Examples of some of the plant communities observed on St. Matthew Island are presented below. The names of vascular plants are according to HULTÉN (1941–1950).

Beach ridges. The stabilized beaches characteristically supported dense stands of *Elymus arenarius* L. ssp. *mollis* (Trin.) (Fig. 2). This association included *Lathyrus maritimus* (L.), *Senecio pseudo-Arnica* Less., and frequently *Poa eminens* Presl. *Angelica lucida* L. was present locally.

Dry lowlands. On the extensive lowlands of the southeastern part of the island, the vegetation consisted mainly of lichens, mosses, and sedges. The common lichens were *Cladonia alpestris* (L.) Rabenh., *C. bellidiflora* (Ach.) Schaer., *C. coccifera* (L.) Willd., *C. carneola* E. Fries, *Cetraria delisei* (Bory) Th. Fr., *C. andrejevii* Oksn., *Sphaerophorus globosus* (Huds.) Vainio, *Thamnolia vermicularis* (Sw.) Schaer., and *Nephroma arcticum* (L.) Torss. Mosses included *Polytrichum strictum* Brid. and *Hylo-*



Fig 2. *Elymus*-association along north beach



Fig. 3. Stabilized beach grown to lichens and *Empetrum nigrum*. An old polar bear trail overgrown by *Empetrum* is visible.

comium splendens (Hedw.) Schimp. Among sedges and rushes were *Carex nesophila* Holm, *C. spectabilis* Dew., *Luzula arcuata* (Wahlenb.), and *L. nivalis* (Laest.) Beurl. var. *latifolia* (Kjellm.). A willow, *Salix crassijulis* Trautv., occurred rather commonly, and *Empetrum nigrum* L. also was present. A specimen of *Betula nana* L. was collected in this area by F. H. FAY; his is the only record of dwarf birch on St. Matthew Island.

Lichens and *Empetrum nigrum* formed the main ground cover of the driest part of the old beach separating the largest lake from the sea (Fig. 3). Prominent among the lichens was *T. vermicularis*, which in general had suffered severe fragmentation by the reindeer. Large areas were covered by pure stands of *E. nigrum*, which was invading areas grown almost exclusively to lichens.

Moist lowlands. Moist, relatively well drained lowlands, in which the soil was a gravelly loam, supported a dense vegetation. The prominent plants were *Deschampsia caespitosa* (L.) Beauv. ssp. *orientalis* Hult., *Poa eminens*, *Arctagrostis latifolia* (R. Br.) Griseb., *Carex* ?*Ramenskii* Kom., *Juncus castaneus* Smith, *Rumex arcticus* Trautv., *Cochlearia officinalis* L. ssp. *oblongifolia* (DC.) Hult., and *Polygonum viviparum* L.

Also in such areas were *Equisetum arvense* L., *Luzula multiflora* (Retz.) Lej., *Artemisia arctica* Less., *Sedum Rosea* (L.) Scop. ssp. *integrifolium* (Raf.) Hult., *Arnica Lessingii* Greene, *Saxifraga punctata* L. ssp. *Nelsoniana* (D. Don) Hult., *Arenaria physodes* (Fisch.), *Claytonia sarmentosa* C. A. Mey., *Papaver alaskanum* Hult., *Lychnis apetala* L., and *Valeriana capitata* Pall.

Where more water was present, the following were prominent: *Poa leptocoma* Trin., *Carex Lachenalii* Schkur, *C. nesophila*, *Primula tschuktschorum* Kjellm., *Pyrola minor* L., *Pedicularis Langsdorffii* Fisch., *Salix polaris* Wahlenb., *Cochlearia officinalis* ssp. *oblongifolia*, *Epilobium anagallidifolium* Lam., *Saxifraga punctata* ssp. *Nelsoniana*, and *Caltha palustris* L. var. *arctica* (R. Br.) Huth.

Wet lowlands. In wet meadows and along margins of ponds were dense stands of sedges, including *Eriophorum angustifolium* Honck., *Carex aquatilis* Wahlenb. var. *stans* (Drejer) Boott, and *C. Lachenalii* (Fig. 4). *Arctophila fulva* (Trin.) Anders. grew abundantly in the shallow ponds.

Peat mounds in wet areas were grown largely to mosses, including *Sphagnum squarrosum* Crome, *Polytrichum strictum*, and *Hylocomium splendens*. Other species present on such mounds were *Empetrum nigrum*, *Rubus arcticus* L., *Cornus suecica* L., and *Carex* ssp. On the lower areas surrounding the mounds mosses and sedges grew, generally to the exclusion of other forms.

Moderately wet areas, sometimes at higher elevations, supported a variety of plants. Among the mosses were *Sphagnum* sp., *Tetraplodon minoides* (Hedw.) BSG, and *Calligeron stramineum* (Brid.) Kindb. Other species were *Poa arctica* R. Br., *Festuca rubra* L., *Arctagrostis latifolia*, *Luzula arcuata*, *Salix reticulata* L., *S. ovalifolia* Trautv., *S. crassijulis*, *Saxifraga Hirculus* L., *S. hieracifolia* Waldst., *Oxyria dignya* (L.) Hill, *Sanguisorba stipulata* Raf., *Cardamine pratensis* L., *Petasites frigidus* (L.), and *Cerastium Beeringianum* C. & S.

Lower slopes. The vegetation of the lower slopes in general resembled that of lowlands having a comparable degree of moisture (Fig. 5). On well drained areas were abundant mosses, lichens, and *Empetrum nigrum*, *Rubus arcticus*, *Salix* ssp., *Cornus suecica*, *Carex* ssp., and grasses. In moister areas, prominent species were *Pedicularis verticillata* L., *Potentilla egedii* Wormskj. var. *groenlandica* (Tratt.) Polunin, *Minuartia arctica* (Stev.) Aschers. & Graebn., *Lagotis glauca* Gaertn., and *Artemisia globularia* Cham.

Higher slopes and mountain tops. The composition of the vegetation on the higher slopes varied with the amount of moisture present and with the character of the



Fig. 4. Wet lowland habitat. Prominent plants shown are *Arctophila fulva* and *Eriophorum angustifolium*.



Fig. 5. Lower slopes, near southeast end of St. Matthew Island

soil. Lichens included *Ramalina scoparia* Vain., *Lobaria linia* (Ach.) Rabenh., *Nephroma arcticum*, *Stereocaulon vesuvianum* Pers., *Alectoria ochroleuca* (Ehrh.) Mass., *Parmelia omphalodes* (L.) Ach., and *Ochrolechia* sp. Prominent mosses were *Drepanocladus uncinatus* (Hedw.) Warnst., *Hylocomium splendens*, *Pleurozium schreberi* (Brid.) Mitt., *Dicranum fuscescens* Turn., *Bryum* sp., and the hepatic, *Gymnomitrium corallioides* Nees. The vascular plants included *Lycopodium Selago* L., *L. alpinum* L., *Poa Komarovii* Roshew., *P. arctica*, *Carex podocarpa* R. Br., *Empetrum nigrum*, *Salix polaris*, *Senecio atropurpureus* (Ledeb.) Fedtsch., *Sedum Rosea* ssp. *integrifolium*, *Saussaurea viscida* Hult., and *Polygonum Bistorta* L. ssp. *plumosum* (Small) Hult.

Few species were present on exposed mountain tops. Here, *Dryas octopetala* L. ssp. *punctata* (Juz.) Hult., covered large areas, and willows were common.

There was little soil on high, rocky ridges where frost action had produced pavmenting and rock polygons. Lichens of the genus *Umbilicaria* covered the rocks in situations partially protected from the wind. In less exposed rocky areas, usually at somewhat lower altitudes, mosses and lichens, and *Saxifraga bronchialis* L. ssp. *funstonii* (Small) Hult. were common.

Fauna

Invertebrates. We attempted a general survey of the invertebrate fauna in 1954. Certain organisms occurred in great numbers, but as would be expected on a small island at this latitude, the number of species represented was relatively small. The collections included several undescribed species as well as others of uncertain status.

Aquatic invertebrates abounded in some of the smaller lakes and ponds. A large hydra, not identifiable after preservation, was present on submerged vegetation. A

species of rhabdocoel turbellarian, subsequently described as *Mesostoma andrewsi* Hyman, 1957, was found in wet tundra vegetation and along small streams (the type locality was incorrectly designated in the published description).

Microcrustacea were abundant in small ponds and in other habitats. Of the Copepoda, the suborder Calanoida was represented by two species, *Diaptomus pribilofensis* Juday and Muttkowski and *Eurytemora gracilicauda* Akatova (see WILSON and TASH 1966). Species of Cyclopoida included *Cyclops kolensis* Lilljeborg, recently determined to have a holarctic distribution (E. B. REED, Pacific Science, in press). Several species of Harpacticoida were identified by Mrs. M. S. WILSON (personal communication), and *Paracamptus reggiae* Wilson, 1958, was described from this material. One species of Cladocera, *Eurycercus lamellatus* (Müller), has been reported from these collections (REED, 1962, p. 39). Ostracods were numerous. Among these was the widely distributed *Candona subgibba* Sars, of which the male hitherto was unknown (M. S. WILSON, personal communication).

Amphipods were present in both ponds and small streams, and a large isopod, *Idothoea entomon* (L.), occurred abundantly in the largest lake. Aquatic larvae of insects (Trichoptera and Plecoptera) were common in small streams. The two species of freshwater molluscs recorded were *Pisidium liljeborgi* Clessin and *Gyraulus deflectus borealis* (Westerlund).

The collection of insects included more than 70 species belonging to nine orders (Collembola, Plecoptera, Trichoptera, Hemiptera, Coleoptera, Lepidoptera, Hymenoptera, Diptera, and Siphonaptera). Diptera, Hymenoptera, and Coleoptera, represented by 22, 14, and 8 genera, respectively, were the most abundant. Many of the identified species are of holarctic distribution, or have been recorded from localities in Alaska or in Canada. The Hymenoptera, particularly some of the small, apterous forms, seem to show some tendency toward endemism, although this cannot be certainly determined until the fauna of the amphiberian region becomes more adequately known (W. R. M. MASON, personal communication).

The insects most in evidence were flies, including *Cynomyopsis cadaverina* (R.-D.), *Cynomya mortuorum* (L.), and particularly *Scatophaga* species. Only one species of biting fly, *Prosimulium ursinum* Edw., was noted. Large bees, *Bombus balteatus* Dahlb., were active on brighter days. Insects were most readily collected on bright or sunny days, when many were attracted to the flowers of *Angelica lucida*. For example, caddis flies (Trichoptera) representing three genera (*Glyphopsyche*, *Limnephilus*, and *Grensia*) were obtained on these umbels, but only the larvae of *Lepidostoma* sp. were discovered in aquatic habitats.

The spiders obtained were *Erigone arctica* (White), *Bathypantes pallida* (Banks), and unidentifiable females of two species belonging to the subfamily Erigoninae. No attempt was made to collect free-living mites. *Succinea strigata* Pfeiffer was the only species of terrestrial mollusc observed.

Vertebrates. Four species of freshwater fishes were taken on St. Matthew Island. Trout, *Salvelinus malma* (Walbaum), were numerous in streams and in the largest lake, where they were feeding mainly on isopods. Also present in this lake were two species of sticklebacks, *Gasterosteus aculeatus* L. and *Pungitius pungitius* L. A partially digested fish from the stomach of a trout was identified as a blackfish, *Dallia pectoralis* Bean, by Dr. N. J. WILIMOVSKY. Another trout, *Salvelinus alpinus* (L.) is now known to occur on St. Matthew Island (N. J. WILIMOVSKY, personal communication). A parasitic copepod, *Salmincola* sp., was found commonly on the trout. The numerous endoparasites of the trout have not been identified.

Birds of three species were collected around the St. Matthew Islands on COOK's last voyage (STRESEMANN, 1949), and additional specimens were obtained by VON KITTLITZ (1858). TOWNSEND in 1887 mentioned a few species. The ornithological

findings of the Harriman Alaska Expedition were never published, but the records of A. K. FISHER, a member of this party, were incorporated in the list of 36 species reported by HANNA (1917). Twenty-eight species were identified by KLEIN (1959), who listed in addition seven recorded in the unpublished notes of F. L. BEALS. We identified 34 species in 1954, including five not previously recorded from these islands: *Arenaria melanocephala* (Vigors), *Numenius phaeopus* (L.), *Erolia melanotos* (Vieillot), *Erolia bairdii* (Coues), and *Stercorarius pomarinus* (Temminck).

The avian fauna of these islands comprises less than 40 breeding species, among which members of the orders Anseriformes and Charadriiformes predominate. Nearly all are species having a holarctic distribution. One, *Plectrophenax hyperboreus* Ridgway, is endemic, breeding exclusively on these islands. A subspecies of rosy finch, *Leucosticte tephrocotis umbrina* Murie, nests only on these and the Pribilof Islands.

The terrestrial mammalian fauna originally included three species, the polar bear, *Ursus maritimus* Phipps, the arctic fox, *Alopex lagopus* L., and a vole, *Microtus abbreviatus* Miller. The polar bears have been destroyed, and domestic reindeer, *Rangifer tarandus* L., have been introduced.

We found, in trapping extensively in diverse habitats, no evidence of the occurrence of any small mammals besides *M. abbreviatus*, nor did F. H. FAY.

Polar bears were seen on the St. Matthew Islands by members of the Billings Expedition; SAUER (1802, p. 236) remarked that "Several white bears swam around the ship while we weret at anchor, and three of them made many attempts to get up the ship's side; but at length they all swam to the large island." Von KITTLITZ (1858), who also observed these animals, concluded (p. 302) that „Diese Thiere werden mit den Eisschollen des Winters in Menge nach den sämtlichen Inseln des Beringschen Meeres gebracht, wo sie zumal auf einer so nördlich gelegenen wie diese leicht in den Fall kommen, auch den Sommer über zurückzubleiben.“ ELLIOTT (1882, p. 117) estimated that not less than 250 to 300 bears were present on the two larger islands in August, 1874. NELSON and TRUE (in NELSON, 1887, p. 254) considered the polar bears to be permanent residents. Although bears were present on Hall Island as recently as September, 1885 (TOWNSEND, 1887), and some were seen there by DAWSON (1894, p. 138) in 1891, none was observed by members of the Harriman Alaska Expedition in July, 1899 (BURROUGHS, 1902, p. 113). HANNA (1920, p. 121) stated that "... bears were found up until sometime in the 90's when a party from the revenue cutter CORWIN landed and shot 16." Two bears were reportedly seen on St. Matthew Island by men of the Coast Guard during the winter of 1942-43 (G. W. PLAYDON, personal communication). Old bear trails, overgrown by vegetation but still visible in 1954 (Fig. 3), attest to the former abundance of these animals.

The occurrence of foxes on the St. Matthew Islands also was first reported by SAUER (1802, p. 236). No further recorded observations appear to have been made until 1899, when members of the Harriman Alaska Expedition collected specimens. MERRIAM (1900) described the fox from these islands as a distinct species, *Vulpes hallensis* Merriam. It was designated *Alopex lagopus hallensis* by RAUSCH (1953a). Although this fox is still considered to be an endemic subspecies (cf. HALL and KELSON, 1959, p. 854), the population cannot be geographically isolated because of opportunities for immigration and emigration during the winter when the islands are surrounded by pack ice.

Although the St. Matthew Islands had been designated a National Wildlife Refuge in 1909, reindeer were introduced by the United States Coast Guard in 1944, when on 20 August, 5 males and 24 females from the herd on Nunivak were released on St. Matthew Island. An adequate survey was not made before the introduction, but F. L. BEALS (unpublished notes) estimated that the island could support 400 animals. At least 400-500 reindeer were present in the summer of 1954, when damage to the

vegetation was clearly evident locally in the areas utilized as winter range. By the summer of 1957, the reindeer numbered about 1350, and further deterioration of the winter range had taken place (KLEIN, 1959). The herd had increased to about 6000 by the summer of 1963. In the following winter, most died, leaving only 42 by the summer of 1966 (D. R. KLEIN, personal communication). If those remaining are unable to survive, eventual recovery of the vegetation on St. Matthew Island can be expected.

The species of marine mammals observed in surrounding waters or identified from remains found on the beaches have been listed by HANNA (1920) and by KLEIN (1959). In addition, we found the skull of a harbor porpoise, *Phocaena vomerina* (Gill), on the beach of St. Matthew Island. COOK (1822, p. 693) reported seeing sea otters there on 23 September 1778.

Notes on the Biology of *Microtus abbreviatus*

The first published reference to the occurrence of microtine rodents on the St. Matthew Islands appears to be that of MAYNARD (1876), who mentioned (p. 19) that "lemming" were present. TOWNSEND (1887, p. 97) discussed the vole briefly under the name *Arvicola obscurus* Eversmann [= *Arvicola obscura* Eversmann, 1841 = *Microtus arvalis obscurus* (Eversmann, 1841)]. The single specimen obtained by TOWNSEND on Hall Island in September, 1885, provided the basis for the description of *M. abbreviatus* by MILLER (1899). Additional specimens were collected on both Hall and St. Matthew Islands in July, 1899, by the Harriman Alaska Expedition. *M. abbreviatus* was redescribed from this material by MERRIAM (1900), who at the same time distinguished the vole on St. Matthew Island as a subspecies, *M. abbreviatus fisheri* Merriam.

The observations reported here concern *M. abbreviatus fisheri*, of which we collected 238 in 1954, besides the 12 captured alive. The offspring of the captives were studied in the laboratory. In 1963, F. H. FAY examined 12 voles in the field and brought two males alive to the laboratory.

General Characteristics: *Microtus abbreviatus* is a relatively large, short-tailed vole closely resembling *M. gregalis* Pallas in external characteristics. In adults, the length of the tail ranged from 27 to 32 mm, comprising from 15.8 to 18.8 per cent (av. ca. 17 per cent) of the total body length. The maximum size recorded for males was 78.9 g with a total length of 176 mm, and for females (non-pregnant), 76.3 g with a total length of 171 mm. In captivity the males tend to become heavier, because of accumulated fat. The maximum weight recorded for a laboratory-reared animal was 92.4 g for a male 9 months, 11 days old. None of the captive females equaled the largest wild females in weight.

Adult voles in fresh pelage (late August — early September) are rather brownish dorsally (near Saccardo's Umber; capitalized names of colors are according to Ridgway, 1912), shading to more ochraceous (near Clay Color) on the sides, rump, and anterior part of the face. The ear-tufts likewise are more ochraceous. Dorsally, the feet are paler, near Buffy Brown. The ventral surface, including that of the tail, is buffy. A single melanistic individual was trapped on 29 August 1954. This animal, an adult female weighing 62.9 g with a length of 169 mm, was black dorsally, with a slight brownish tinge on the sides. The ear-tufts, face, and dorsal surface of the feet were brownish.

Both in color and pattern, *M. abbreviatus* is very nearly indistinguishable from *M. gregalis miurus* Osgood (from the Kenai Peninsula, Alaska). *M. g. miurus* tends to be slightly more greyish ventrally and on the dorsal surface of the tail and feet,



Fig. 6. Vole in watchful position at mouth of burrow



Fig. 7. View to the northwest across lowlands near southeast end of St. Matthew Island. The largest lake is at upper left. Zones of optimum habitat of *M. abbreviatus* here in 1954 are: A = *Elymus* zone on beach ridge, B = zone of driftwood, C = lowland with greatest density of population. Distance from highland to highland is about 6 km.



Fig. 8. Driftwood zone along north beach

and lacks the well defined ochraceous area on the sides of the face in *M. abbreviatus fisheri*. MERRIAM (1900) stated that *M. a. abbreviatus* tends to be more grey than *M. a. fisheri*.

During the time of our observations, the voles were diurnally active under all conditions of weather excepting heavy rain. Their behavior in general was similar to that of *M. gregalis* on the Alaskan mainland. In walking through areas densely populated by *M. abbreviatus*, one was preceded by the voles' high-pitched, musical call, possibly a sound of alarm. This call was usually made by the animals just before they entered the burrow (Fig. 6). However, captives often uttered a similar sound when undisturbed. As noted in the captive colony, these voles also made a squeaking sound when fighting, copulating, or when handled. Wild voles rarely attempted to bite when captured.

Habitat: In late summer of 1954, when the density of the population was high, the voles occurred in maximum numbers in the moist lowlands and on the lower slopes. They also were numerous in the *Elymus*-association along beach ridges (Fig. 2) and in the zone of driftwood along the lowland separating the largest lake from the sea (Figs. 7 and 8). They did not inhabit the dry lowlands nor areas with much standing water, although large colonies were sometimes located along the banks of small streams or around seepages on the slopes. The voles were never observed in water, nor were any runways found which passed in part through shallow water as, for example, one often finds in wet habitat occupied by *M. oeconomus* Pallas.

On the higher slopes, favorable habitat was occupied to elevations of about 245 m. The colonies were in moist, well drained situations as well as around water-filled depressions or seepages. Burrows were made in rocky outcroppings adjacent to well vegetated areas, but not in rocky places where vascular plants were few.

In the summer of 1963, when the voles were scarce, F. H. FAY found residual colonies in the driftwood bordering the north beach, and on some of the lower slopes, and he observed that much previously occupied habitat in the lowlands had been badly damaged by the activity of the reindeer.

In 1954, in areas of optimum habitat the burrows were numerous and close together, with few exposed runways (Fig. 9). The appearance of such areas in general resembled that of alpine habitat occupied by *M. gregalis*. In the zone of driftwood, the voles' runways extended across open areas from one burrow to another, but rarely exceeded a few meters in length.

In the moist, gravelly loam of the lowlands, burrows had been excavated at depths from 10 to 20 cm beneath the surface. Interconnected systems extending over areas of 4.5 to 6 m in diameter were evidently occupied by family groups. Each system had several openings to the surface, around some of which were accumulations of feces. No cavities containing feces were found underground. Nest chambers contained dry grasses and sometimes the dried roots of *Elymus*. Larger excavations, as much as 50 by 26 cm, still empty in mid-August, presumably were chambers for storage of food.

Feeding and Diet: The voles fed at any time during the day. Emerging cautiously from the burrow, individuals would at first sit erect and look about, at the same time uttering their characteristic call; if not alarmed, they would begin to feed in an apparently random manner in the vicinity of the burrow (Fig. 10). After feeding briefly, they often ran quickly to the burrow, only to emerge soon and resume their former activity. Nothing was learned of their behavior at night.

Their diet undoubtedly included a variety of plants, but few were identified through observation of feeding. Often in dense stands, young growth of a grass, *Deschampsia caespitosa*, was heavily utilized. Other important species were *Artemisia arctica*, *Rumex arcticus*, *Salix ovalifolia*, *S. crassijulis*, and especially, *Sedum Rosea*. One animal was seen eating the flowers of *Saxifraga Hirculus*.

Diet in captivity. At the time the voles were brought to the laboratory, we had not yet established a standardized method for the maintenance of microtine rodents in captivity. The diet provided was excessive in variety and consisted of about equal



Fig. 9. Typical burrows of *M. abbreviatus*



Fig. 10. Vole feeding near burrow. Prominent plant is *Sedum Rosea ssp. integrifolium*.

parts of cracked corn (maize), rolled oats (oatmeal), compressed dry pellets of alfalfa, and a ration in pellet form (commercially prepared for laboratory mice). Head lettuce was supplied daily, and carrot was always available. The animals received no water besides that contained in the lettuce and carrot.

Reproduction and Development

In the field 133 females and 105 males were examined. The observed range in size, as indicated by weight, is shown in Fig. 11. The distribution according to body length was comparable, but only about 100 (those prepared as museum specimens) were measured. Four cohorts of young animals evidently were present, of which the largest probably represented the first summer (June) litters.

As determined by the presence of placental scars or embryos, or by other findings, 30 of the 133 females (23 per cent) were breeding during the summer of 1954. These ranged from 45 to 77 g in weight; none of smaller size was sexually mature. Three weighing more than 45 g (45.7; 46.7; 47.8) had not attained sexual maturity. The 21 females whose weights exceeded 55 g were considered to be adults born in summer, 1953, or in the case of the largest, possibly earlier.

Placental scars were present in 20 animals. Of these, accurate counts could not be obtained in two, and ten scars were found in a pregnant vole containing five embryos. Of the remaining 17, 13 had from two to seven scars, probably indicating the birth of a single litter, while four had 10, 11, 12, and 18, respectively, indicating birth of two or three litters. The average number of placental scars was about 7 (6.9). A highly vascular uterus in two animals (62.4 and 67.2) probably was an indication that they were in condition for breeding. One enlarged uterine horn was noted in a subadult

(45.0 g) in which evidence of pregnancy otherwise was not detected. A relatively high proportion of the females was apparently uniparous; this suggests that breeding had been suppressed after they had produced a litter in the spring.

Since the annual period of breeding of *M. abbreviatus* can be expected to extend from late May to about mid-August, our observations were undertaken too late in the season to find many pregnant animals. Five were captured during the period 5–10 August, and three, late in the month (18th, 25th, and 29th). All but one of the pregnant voles were adults, ranging in weight from 60.4 to 77 g; the exception, possibly a subadult, weighed 47.1 g. The three collected in late August were large adults. The number of embryos ranged from five to seven (five in two animals; six in three; seven in three), with an average of about six. Two of those pregnant were lactating.

The findings in one of the pregnant voles were unusual. This animal, trapped on 29 August and weighing 77 g, contained five embryos, of which one was being resorbed. The remaining four were ostensibly normal, but two were twins (i. e., both attached to a single placenta of characteristic size and appearance). The twins were small, 17 mm in crown-rump length, while the other two measured 22 mm in this dimension.

The series of 105 males included 11 adults, readily distinguishable by their large size (Fig. 11). Weights of these ranged from 65.5 to 78.9 g, whereas weights of young of the year did not exceed 51.6 g. All of the adult males were in breeding condition, with testes measuring from 13.0 to 14.5 by 7.5 to 9.5 mm. Seven of the latter were collected during the period 5–19 August, and the remainder from 25 August to 2 September. As indicated by testicular size (11 to 13 by 6 to 9 mm), only three subadults appeared to have been capable of breeding; these weighed 40.7, 46.3, and 48.8 g.

Captive animals. Captured as subadults, the voles did not begin to breed in the laboratory until early spring of 1955. In the meantime, one had been used experimentally, and a female died on 6 March 1955. Of the remaining five pairs, only two produced young, and most of the litters obtained were the offspring or descendants of a single pair. Because of high mortality, discussed below, and lack of reproduction, the colony could not be maintained after late 1957.

The voles were paired in the winter of 1954–55, in cages containing wood shavings as litter, and cotton for nesting. Two pairs showed signs of breeding around 1 March 1955; the males pursued the females persistently, both uttering squeaking sounds at frequent intervals. Copulation was observed in one cage on 1 March, but the two pairs did not produce young until 3 April and 28 May, respectively. On 6 May, the largest of the original males weighed 100 g.

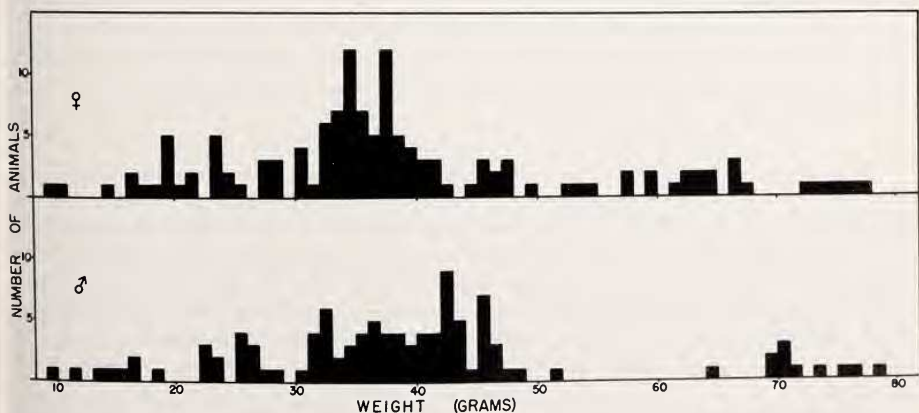


Fig. 11. Distribution by weight of 238 specimens of *M. abbreviatus*

The voles constructed rather large, rounded nests in which the young were concealed. Both parents attempted to defend the young when the nest was disturbed, but the female was the more aggressive. As indicated by the shortest intervals between litters, the gestation period was 21 days (two observations). The litters were in general rather widely spaced, and productivity was low compared with results obtained with other microtine species under the same conditions. In all, the colony produced 65 young in 26 litters. Size of litters ranged from one to five, with a mean of only 2.5 and a mode of 2. A comparable, consistent reduction in average size of litters of captives as compared with that recorded in wild individuals has not been observed by us in other species. This probably was a manifestation of the lowered vitality characteristic of this colony of *M. abbreviatus*.

The weight of the voles at birth was not determined; average individual weights for a litter of four during the first weeks of life were as follows: seven days, 7.5 g; 14 days, 11.4 g; 21 days, 18.8 g; 26 days, 25.0 g. Growth-curves obtained after the animals reached an age of about a month were considered to be atypical, as explained below.

The young were well furred by the sixth day, by which time they usually ran from the nest when disturbed. The eyes opened on the 11th day, and the animals were weaned by about the 15th day. The first molt, from juvenile to subadult pelage, began at an age of about a month, and molt into adult pelage began at about three and one-half months. The minimum time required for the voles to attain sexual maturity was not determined, since reproduction invariably was delayed until the animals were several months old.

Fluctuations in Numbers

The few recorded observations indicate that under natural conditions the numbers of *M. abbreviatus* fluctuate widely, but whether the fluctuations are regularly cyclic cannot be demonstrated from existing data. MAYNARD (1876) and ELLIOTT (1882) provided no information about numbers of voles they observed. Many burrows were found on Hall Island in September, 1885, by TOWNSEND (1887); that he secured only one specimen (p. 97) probably indicates that voles were scarce. They evidently were numerous when the Harriman Alaska Expedition visited the islands on 14–15 July 1899. Many runways were seen in July, 1916, by HANNA (1920), who stated that evidence of recent activity was not present. BEALS (unpublished notes) recorded on 1 July 1944 that the voles were "abundant everywhere" on St. Matthew Island. The population had probably attained near maximum density on St. Matthew Island in the summer of 1954, but it was again "very low" in July–August, 1957 (KLEIN, 1959, p. 44). F. H. FAY observed only small, isolated colonies in July, 1963.

Predation

The predators of *M. abbreviatus* represent few species, of which the most important are the arctic fox, the long-tailed jaeger, *Stercorarius longicaudus* Vieillot, and in some years, the snowy owl, *Nyctea scandiaca* (L.). Voles might be taken occasionally by glaucous gulls, *Larus hyperboreus* Gunnerus, which nest on the islands, and perhaps also by migrating jaegers of other species [*S. pomarinus* and *S. parasiticus* (L.)]. No doubt the polar bears consumed many voles in summers when the rodents were abundant.

As would be expected, voles were a major food for young foxes in the dens during the summer of 1954. Foxes were observed hunting in areas having high populations

of voles, and a female shot on 27 August, as she was approaching a den with food, was found to be carrying nine recently killed voles. During July, 1963, when voles were few, F. H. FAY found that the foxes were eating carrion, primarily reindeer, and young birds. He found no voles in the stomachs of the 17 foxes he examined.

Both long-tailed jaegers and snowy owls appear to be erratic in their occurrence on the St. Matthew Islands. A long-tailed jaeger containing two voles was shot by A. K. FISHER on 14 July 1899 (HANNA, 1917, p. 407). No jaegers were observed by HANNA in 1916. BEALS found long-tailed jaegers to be "occasional" in June, 1944, and to be seen "frequently" in July. They were not recorded in 1957 by KLEIN (1959). At least one was seen by F. H. FAY in 1963.

During August, 1954, long-tailed jaegers were common. They were feeding largely upon the abundant berries of *Empetrum nigrum*, and none was observed attempting to capture voles. However, they occasionally carried away dead voles in mouse-traps.

Snowy owls may be numerous in some years. According to A. K. FISHER (cited in HANNA, 1917), "several" were seen on Hall Island in July, 1899, where a nest containing four young was found. HANNA (1917) saw only traces of owls (feathers and regurgitated pellets). F. L. BEALS stated that owls were numerous in 1944. We observed none in 1954 and found only a single regurgitated pellet of considerable age; as indicated by its small size, it probably came from a hawk. No snowy owls were seen by KLEIN or by FAY.

Parasites and Disease

Few abnormalities and no evidence of disease caused by microorganisms were found in the examination of 228 voles on St. Matthew Island in 1954. A recently weaned vole (12.0 g) was found dead, but the cause of death was not determined. Small areas of focal necrosis of unknown origin were found in the liver of three animals, all subadults. One vole had lost the greater part of the tail, and one exhibited a healed fracture of a zygomatic arch. Ectoparasites were not abundant, and the helminth fauna included only species regularly found in *Microtus* spp. at higher latitudes (cf. RAUSCH, 1957). The captive animals were affected by various disorders, most important of which were epithelial papillomatosis of the stomach and a pulmonary disease of probable bacterial origin.

Helminths. The following species of helminths were recorded from *M. abbreviatus*: (Cestoda) *Paranoplocephala omphalodes* (Hermann, 1783) in 16 (7 per cent); *P. infrequens* (Douthitt, 1915) in 5 (2.2 per cent); *Andrya macrocephala* Douthitt, 1915, in 14 (6 per cent); *A. arctica* Rausch, 1952, in 23 (10 per cent); unidentified cestodes (immature anoplocephaline species) in 6 (2.6 per cent); *Taenia crassiceps* Rudolphi, 1810 (larval stage) in 2 (0.8 per cent); (Nematoda) *Heligmosomum costellatum* (Dujardin, 1845) in 147 (64.5 per cent). Data on the occurrence of intestinal parasites in relation to age (weight) of the host are summarized in Table 2.¹

The young voles might be exposed to infection by these helminths soon after they are weaned, probably at an age of 15 to 20 days. The life cycle of the nematode, *H. costellatum*, is direct, and infective larvae might be numerous wherever feces are deposited by older animals. That exposure to these larvae occurs relatively early in life is indicated by the finding that more than half of the younger animals were infected by the time they had reached an age of about 4–6 weeks (25–35 g). Thereafter the rate of infection increased with age, as did the average number of worms per infected animal (Table 2).

¹ Subsequent study of these nematodes by Dr. A. CHABAUD and his coworkers at the Muséum d'Histoire Naturelle, Paris, indicates that the species is not *H. costellatum*, but evidently an undescribed species of *Heligmosomum*.

Table 2

Occurrence of helminths in *M. abbreviatus* according to age (weight) of host

Weight Class (grams)	Total voles per class	Number negative for helminths	<i>H. costellatum</i>		Cestodes	
			Number Infected	Number per animal Range	Number per animal \bar{M}	Number Infected
6-15	7	7	0	—	—	0
16-25	30	26	1	—	—	3
26-35	61	17	38	1- 30	6.3	11
36-45	79	11	63	1- 34	8.5	13
46-55	20	1	18	1- 22	5.9	9
56-65	12	2	9	2- 49	11.5	5
66-80	19	0	18	1-149	22.9	11
Totals	228	64	147			52
		(28.0%)	(64.5%)			(22.8%)

The highest rates of infection with *H. costellatum* were observed in voles taken in well drained, heavily vegetated areas. Lowest rates of infection for helminths of all species were recorded in animals from the zone of driftwood along the north beach.

The cestodes from the intestine of the voles were all anoplocephaline species whose infective stage presumably occurs in oribatid mites. Thus, exposure to infection could be expected as soon as the young voles begin to feed around the burrows. Immature specimens of *A. macrocephala* (50 to 90 mm long, with as many as 250 segments) were found in three voles in the weight range of 16-25 g, indicating that infection had occurred soon after weaning. A gravid specimen of *A. macrocephala* (152 mm long) was found in one animal weighing only 28.4 g (see below). Excluding the small, immature cestodes, which were not identifiable, the average number of each of the respective species of cestodes was less than two per infected vole. The number of immature cestodes occurring with a single gravid specimen (excluding *P. infrequens*, which is found usually in the ileo-cecal valve) ranged from one to three per animal in all cases but one, when six were present. In one instance, four gravid specimens of *A. arctica* were present; otherwise, the number of gravid cestodes of a single species did not exceed two per animal. As with *H. costellatum*, the rate of infection with anoplocephaline cestodes increased with age of the host, but there was no comparable increase in average number of worms. Multiple infections, comprised of gravid cestodes of two species, were observed only in the oldest animals (weight range 65-80 g), with the following combinations: *P. omphalodes* and *P. infrequens*, two voles; *P. omphalodes* and *A. arctica*, one; *P. infrequens* and *A. arctica*, one. More than half of the voles infected by anoplocephaline cestodes also harbored *H. costellatum*.

T. crassiceps is one of the species of cestodes for which microtine rodents serve as intermediate host and which occur as adults in animals regularly preying upon such rodents. In the intermediate host, *T. crassiceps* reproduces asexually by means of exogenous budding; the resulting aggregations of vesicles usually are found subcutaneously or in the thoracic or abdominal cavities of voles. The two infected specimens of *M. abbreviatus* were large adults (71.8 and 76.9 g), having respectively 150 and 470 discrete vesicles situated subcutaneously in the ventral thoracic region.

Adverse effects attributable to helminthic infection were noted in only one case. A subadult vole (28.4 g), found sitting in a crouched position with erected hair, made no attempt to escape when approached. Examination disclosed a large specimen of *A. macrocephala* (152 mm long; 5 mm maximum width) which had passed from its

normal habitat in the small intestine into the lower part of the alimentary canal. Partially protruding from the anus, the cestode was occluding the lower intestine, with the result that death of the vole probably would have ensued within a few hours. Another vole (33.0 g) harbored two large specimens of *P. omphalodes*, one of which was in the cecum. Cestodes of certain species, including *A. macrocephala*, evidently are lost spontaneously in the autumn (RAUSCH and TINER, 1949). Massive infections caused by the larval *T. crassiceps* might sometimes hamper the movement of the host sufficiently to increase susceptibility to predation.

Certain species of helminths of wide distribution in the North Pacific region were not found in voles on St. Matthew Island. Among these were two taeniid cestodes, *Taenia polyacantha* Leuckart, 1856, and *Echinococcus multilocularis* Leuckart, 1863. Both occur on the Pribilof Islands and on St. Lawrence Island, where the arctic fox and microtine rodents serve respectively as their final and intermediate hosts. One vole captured in 1954 was exposed to infection by *E. multilocularis* and examined 12 days later. Sections of the liver showed extensive leukocytic infiltration of areas invaded by the embryos, the development of which evidently had been suppressed.

Further interactions between final and intermediate hosts of some helminths on St. Matthew Island are indicated in Table 3, which summarizes findings in arctic foxes.

Ecoparasites. Fleas found on *M. abbreviatus* were *Amalaraeus penicilliger dissimilis* Jordan, a holarctic species which has been recorded from various microtine rodents, and *Megabothris groenlandicus* (Wahlgren), a nearctic species mainly on varying lemmings (*Dicrostonyx*) (HOLLAND, 1963). Both have been recorded from *M. gregalis* in Alaska (RAUSCH, 1964). Parasitic mites included *Hae-mogamasus alaskensis* Ewing, *Laelaps (Hyperlaelaps) kochi* Oudemans, and *Laelaps clethrionomydis* Lange. *L. clethrionomydis* is a palaearctic species associated with

Table 3

Some parasite-host relationships as indicated from helminths in 22 arctic foxes on St. Matthew Island

Species	Number foxes Infected	Intermediate host
Cestoda:		
<i>Schistocephalus solidus</i> (Müller, 1776)	1	<i>Pungitius pungitius</i>
<i>Diphyllbothrium</i> spp.	7	<i>Salvelinus</i> spp.; possibly <i>Dallia pectoralis</i>
<i>Mesocostoides</i> sp.	9	<i>Microtus abbreviatus</i>
<i>Taenia crassiceps</i> (Zeder, 1800)	11	<i>M. abbreviatus</i>
Nematoda:		
<i>Toxascaris leonina</i> (von Linstow, 1902)	20	None
<i>Uncinaria stenocephala</i> (Railliet, 1884)	21	None
Acanthocephala:		
<i>Corynosoma</i> sp.	1	Marine fishes

Microtus gregalis over much of Eastern Siberia (GONCHAROVA, 1956).

Disease in captive voles. The 11 voles remaining in the autumn of 1954 passed the winter in apparent good condition. One of the original females died of undetermined causes in March, 1955, but losses for several months thereafter were few, not exceeding the level usually observed in colonies of microtine rodents in captivity. Only two of the original pairs reproduced, and we resorted to inbreeding in an effort to perpetuate the colony. As a result, most of the voles born in captivity were descendants of two litters produced by one pair. Heavy losses from disease occurred in 1956–57, as described below. In addition, five animals died of hyperthermia following malfunction of the heating system in the laboratory in November, 1956.

After producing a litter of four in April, the female of the first pair died on 30 September 1955, at an age of more than a year (all of the original animals having been born in spring or early summer of 1954). In this animal was found neoplastic involvement of the stomach, a condition which proved to be squamous-cell carcinoma. The male was normal when killed by hyperthermia at an age of more than two years. Gastric tumor did not occur in members of the litter (four females) produced by this pair, all of which lived for more than a year. However, one of these females was mated with an F_2 male descended from the second original pair, and produced a litter of two. These, a male and a female, died of pulmonary disease in September, 1957, at an age of 10 months; the female was found to have a gastric tumor. The father of this litter died on 8 March 1957 of the effects of gastric tumor.

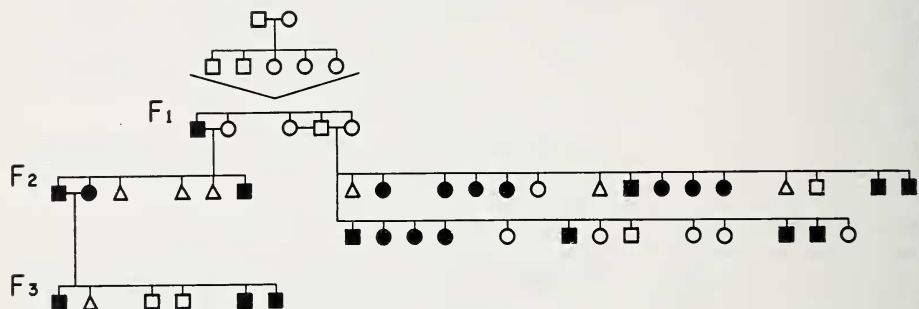


Fig. 12. Observed occurrence (solid symbols) of epithelial papillomatosis of the stomach in the descendants of a single pair of voles from St. Matthew Island

On 4 August 1956 the female of the second pair died, at an age of more than two years, after having produced only two litters (5 May and 9 July 1955). Her spleen contained a large nodule (10 by 8 mm), and focal lesions were present in the liver. The histological findings were consistent with malignant lymphoma (Hodgkin's disease) (Dr. JAMES G. BRIDGENS, personal communication), a disorder not observed again in any of these voles.

The two litters produced by the second pair consisted of two males and three females. After having been kept in a single cage, they were separated for breeding ($\delta\text{♀}$ and $\delta\text{♀♀}$) on 30 September 1955. Beginning in November, 1955, and April, 1956, respectively, the two pairs (one female killed by heat evidently did not breed) produced 34 individuals in 12 F_2 litters. As shown in Fig. 12, epithelial hyperplasia of the stomach occurred in a high proportion (at least 59 per cent) of the F_2 generation. Gastric tumor was the cause of death of 14 animals, and the disorder was found also to exist in six of 11 animals which died of pulmonary disease in September, 1957. Besides the five of the latter group dying of pulmonary disease, one died of hyperthermia, one as a result of dental abnormalities, and one was killed by another vole. Three died soon after birth, and three others also died of unknown causes.

Of the five voles comprising the F_1 generation from the second original pair, all but one lived for more than a year. Causes of death were: ♀, undetermined, March, 1956; ♀, hyperthermia, November, 1956; ♂, gastric tumor, 21 January 1957; ♂♀, pulmonary disease, September, 1957. Epithelial hyperplasia of the stomach was found only in the one animal. One sibling pair of the F_2 generation produced three litters of two each (Fig. 12). Of these, one died of unknown causes at an early age, one of dental abnormalities, and one was killed by another vole; gastric tumor caused the death of two males, and this condition was found in a third which died of pulmonary disease. No F_4 litters were obtained.

Thus, extensive gastric tumor was noted in 25 of the 65 voles born in captivity as well as in one of the 12 animals captured on St. Matthew Island. Since diagnosis was based initially upon macroscopic examination of the animals, early stages of epithelial hyperplasia might have been overlooked. For example, in the case of the vole killed for experimental purposes on 10 October 1954 after having been in captivity for little more than a month, foci of early epithelial hyperplasia with hyperkeratosis and papillomatosis were found in histological sections of the ostensibly normal stomach. Consequently, the actual rate of disease could have been higher than that indicated. Presumably, all affected animals would have died as a result of the gastric disorder, had not other causes of death intervened. The life span of 18 voles which died as a direct result of gastric tumor ranged from 6 to 17 months, with an average of about 11.2 months.

The age at which changes first occurred in the gastric epithelium of laboratory-reared animals was not determined, since younger individuals were not killed for examination. However, few of the F_2 generation exhibited a normal pattern of growth. For voles found to be free of gastric disease, the normal weight at an age of about one year was 60 to 70 g. In a series of seven animals, for example (two litters of the F_2 generation, born 31 May and 29 June 1956), all of which died of gastric disease, growth was significantly retarded after an age of about three months. Some decrease in rate of growth during the fall and winter is characteristic, but the expected vernal increase did not occur over the period February — May, 1957. None of the four of the older litter weighed more than 40 g at the age of a year (one which died on 30 May 1957 weighed only 29.3 g). Some affected animals attained a normal body-length (150 to 175 mm), perhaps indicating later onset of disease, or earlier lesions so localized as to impair gastric function but little. Total weights of animals with advanced disease could be misleading, since the enlarged stomach frequently made up a high proportion of the total (see below).

Based upon diagnoses provided by Dr. JAMES G. BRIDGENS, the histopathological description of the gastric lesions may be stated as follows:

The lesion was a well differentiated epithelial papilloma, characterized by marked papillary formation and extensive production of keratin (Fig. 13). The hyperplastic epithelium formed prominent papillary folds covered by a thick layer of keratin and some parakeratin. Lesions were usually benign, with varying degrees of associated inflammatory change. In some, usually those of longer standing, transformation to a well differentiated squamous-cell carcinoma had occurred. Malignancy was of low grade, but invasion of the underlying tissues by cells showing variation in size, shape, and staining reaction was evident in some areas. Moderate infiltration of the submucosa



Fig. 13. Photomicrograph of tissue section showing typical gastric lesions in stomach of *M. abbreviatus*. Keratinized papillary folds at top project into gastric lumen

and muscularis by lymphocytes and macrophages was frequently seen. Necrosis and abscess formation were not unusual.

A brief description of the structure of the normal stomach of *M. abbreviatus* is necessary to permit an understanding of the mechanism of pathogenesis. As typical for species of *Microtus* (e. g., *M. gregalis* and *M. oeconomus*), the stomach consists of an oesophageal sac on the left, a round glandular area in the fundus, and a pyloric sac (Fig. 14). Although the oesophageal chamber is capable of considerable distension, the stomach in captive voles receiving a concentrated diet generally varies little in size as compared with that of wild voles. In *M. abbreviatus*, the filled stomach fixed *in situ* is about 25 mm in greatest length (fundus to tip of oesophageal sac). The oesophagus enters on the lesser curvature about half way down the length of the oesophageal chamber. The latter is more or less cylindrical, rounded at the proximal end, and about 10 mm in diameter. The pyloric chamber is somewhat rounded, comprising about a third of the volume of the organ. The anterior (dextral) portion of the wall of the oesophageal sac extends posteriad, forming a septum between the two chambers; the margin of the oesophageal chamber extends toward the left of the glandular area in the fundus, where it bends to the right and terminates in a thickened edge, thereby leaving a somewhat U-shaped passage about 5 mm in diameter between the two chambers. At the edge of the glandular area in the fundus, the epithelium of the oesophageal sac terminates in a row of flattened fimbriae which, directed dextrally, slightly overlap the margin of the glandular area. The latter area is concave on its inner surface, 9 to 10 mm in diameter, and surrounded on the pyloric margin by a low ridge derived from the adjacent (non-glandular) mucous membrane.

The oesophageal chamber, including the fimbriae, is lined by stratified squamous epithelium; the edge of that portion forming the septum between the two chambers is muscular, and the radial arrangement of its fibers indicates a capability for considerable modification of its relative position. Stratified squamous epithelium also lines the pyloric chamber, except for a narrow, glandular strip (ca. 5 mm long by 1 mm wide) extending along the lesser curvature as a continuation of the duodenal glands from the pylorus. At the juncture with the duodenum a markedly thickened

muscularis forms a pyloric ring. Folds of stratified squamous epithelium are present in the pylorus. Throughout the stomach, keratin thinly overlays (ca. 0.010 to 0.020 mm thick) the stratified squamous epithelium. The glandular area in the fundus is as much as 1.5 mm in thickness.

In *M. abbreviatus* the massive papillary tumors caused mechanical impairment of gastric function. The findings in less advanced cases suggested that the epithelium first became hyperplastic in the pyloric chamber and around the passage between it and the oesophageal chamber (Fig. 15). Stenosis of the opening between these chambers was often observed, as was occlusion of the pylorus. In older affected animals, the squamous epithelium was almost totally hyperplastic, with the lumina of both gastric chambers largely filled by projecting papillae (Fig. 16). Such papillae, heavily keratinized, attained lengths of 8 mm and greater. The epithelium

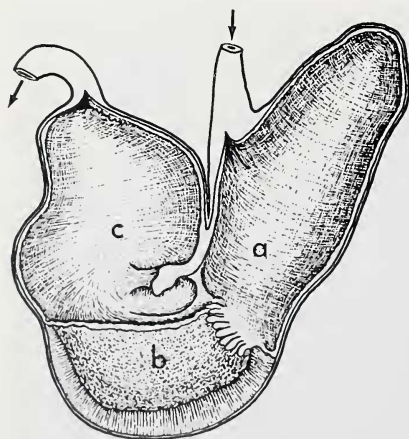


Fig. 14. Diagram of normal stomach of *M. abbreviatus* (captive), showing gross structure — a = oesophageal chamber, b = glandular region of fundus, c = pyloric chamber

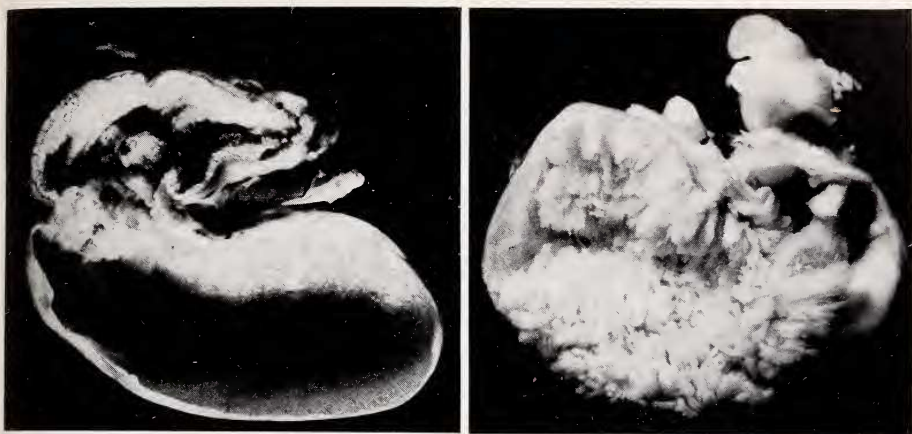


Fig. 15. Stomach of *M. abbreviatus*, showing early stage epithelial hyperplasia involving pyloric chamber and opening of oesophageal chamber. Latter was much distended by impacted food. — Fig. 16. Stomach of *M. abbreviatus*, showing advanced papillary formation.

of the oesophageal sac was usually less involved, giving the impression that it became progressively hyperplastic from the base antieriad. Involvement of the oesophagus was never observed. In cases of longer duration, the stomach was found always to have become enlarged; such enlargement was in part due to thickening of the gastric mucosa, but mainly was a result of great distension of the oesophageal chamber with retained ingesta (Fig. 17). The glandular area in the fundus was never directly involved in the



Fig. 17. Diseased stomach of *M. abbreviatus*, in situ. Arrow indicates areas of secondary inflammation and abscess formation. The oesophageal chamber is much distended.

pathological process, but hyperplasia of the fimbriae and gastric distention sometimes caused a degree of pressure atrophy of its margins.

In voles with advanced disease, subserosal nodules produced by secondary inflammation were frequently observed (Fig. 17). Such inflammation occasionally also involved the upper duodenum near the pylorus. Metastases to other organs were not noted. Secondary complications other than inflammation were unusual. In one case, an abscess 20 mm in diameter arose from the pyloric region on the greater curvature. Occasionally, hairs the voles had ingested were found to have become lodged deeply among the papillae, sometimes evoking a foreign-body reaction; the process in at least one case evidently led to perforation of the gastric wall and peritonitis. A yeast-like fungus, *Candida albicans* (Robin, 1853), was sometimes found in the gastric lesions. Obtained in pure culture, this organism was highly pathogenic for laboratory mice (*Mus*) when injected intraperitoneally.

Aside from the physical deterioration observed in the diseased voles for some time before death, such animals usually exhibited a wetness about the mouth which was pathognomonic for gastric tumor. This sign, possibly present due to gastric obstruction, generally appeared some weeks before death, in one case as early as 2 February in an animal that died on 17 April.

Spontaneously occurring papillary tumors of the gastric epithelium or squamous-cell carcinoma of the stomach evidently have been observed rarely in microtine rodents. The only published record appears to be that of COSGROVE and O'FARRELL (1965), who found epithelial hyperplasia frequently in *Microtus (Pitymys) pinetorum* (Le Conte), in Tennessee. The affected animals had been held in captivity. The lesions in some instances appeared to have been associated with chronic gastritis, possibly secondary to gastric obstruction. However, hyperplasia and squamous-cell carcinoma of the stomach can be readily induced in laboratory mice (*Mus*) by means of carcinogenic agents (STEWART, 1941).

The cause for the high rate of gastric disease in *M. abbreviatus* has not been determined. That a carcinogenic agent was introduced inadvertently in the laboratory is possible, but gastric lesions were extremely rare in other microtine rodents born in the laboratory and kept under similar conditions. From September, 1951, to January, 1966, for example, we recorded *post mortem* findings in 2334 such rodents (not including new-born and small immatures) which had been killed for experimental purposes or had died of various disorders. This series was made up of: *Clethrionomys rutilus* Pallas, 251; *Dicrostonyx torquatus* Pallas ssp., 320; *Lemmus lemmus* Linnaeus, 17; *L. sibiricus* Kerr (including hybrids, *L. sibiricus* x *L. lemmus*), 1082; *Microtus oeconomus* Pallas ssp., 520; *M. pennsylvanicus* Ord, 49; *M. gregalis* Pallas, 95. Among these, hyperplasia of the gastric epithelium was recorded only once, in a specimen of *L. sibiricus* which died on 11 April 1958. Involving mainly the pyloric part of the stomach, the lesion was histologically similar to those found in *M. abbreviatus*; however, an area of acute ulceration was present, and inflammation was more extensive than that observed in lesions in *M. abbreviatus*. Assuming that early-stage lesions might have been overlooked in some of these animals, the rate of occurrence of gastric tumor was nevertheless extremely low compared with that observed in *M. abbreviatus*.

Since the voles on St. Matthew Island comprise a population that is probably quite uniform genetically, having differentiated over a long period of geographic isolation, susceptibility to epithelial hyperplasia of the stomach may be genetically influenced. Moreover, inbreeding in the laboratory may have further influenced the rate of occurrence of this condition. The specific cause for the pulmonary disorder mentioned above was not determined. However, *Klebsiella pneumoniae* (Schroeter, 1886) has been found subsequently to be an important cause of pulmonary disease in our colonies of microtine rodents.

The Taxonomic Status of *Microtus abbreviatus*

M. abbreviatus is derived from a population of voles which evidently was isolated on the St. Matthew Islands during Würm time by eustatic rise in sea level. Either *Microtus oeconomus* or *M. gregalis*, both of which in all probability inhabited the extensive tundra region of the Amphiberingian Refugium (RAUSCH, 1963; REPENNING et al., 1964), appears to have been the progenitor of *M. abbreviatus*. These two species belong respectively to the subgenera *Microtus* Schrank and *Stenocranius* Kashchenko. The subgeneric status of *M. abbreviatus* has not been clearly established.

MILLER (1899), in remarks concerning the affinities of *M. abbreviatus*, stated (p. 4) that it "... is closely related to both *M. kamtschaticus* [= *M. oeconomus kamtschaticus* Pallas] and *M. kadiacensis* [= *M. oeconomus kadiacensis* Merriam = *M. oeconomus operarius* Nelson], though in external appearance its short, densely haired tail gives it a much closer resemblance to the members of the subgenus *Phaiomys*. In cranial and dental characters it differs from *M. kadiacensis* much as it does from *M. kamtschaticus*, since these two species agree closely in palate structure and in the form of the front lower molar." MERRIAM (1900) made no statement concerning the relationship of the species when he described *M. abbreviatus fisheri*. In his revision of the North American species of *Microtus*, BAILEY (1900) stated (p. 44) that "It belongs to the subgenus *Microtus*, and in general character comes nearest to the *operarius* group, from which it is excluded, however, by its unique molar pattern..."

In the same year that the subgenus *Stenocranius* was established by KASHCHENKO (1901), OSGOOD (1901) described *M. miurus* [= *M. gregalis miurus*] from the Kenai Peninsula, Alaska. In his discussion, OSGOOD (p. 65) stated that *M. abbreviatus* was the "nearest known relative" of *M. miurus*, and that "The peculiar enamel pattern like that of *M. abbreviatus* is sufficient to distinguish *miurus* from all other members of the subgenus *Microtus*." NELSON (1931) described *M. muriei* [= *M. gregalis muriei*] from the Brooks Range of arctic Alaska, placing it, with *M. abbreviatus* and *M. miurus*, in the subgenus *Stenocranius*; however, in this group he also included *M. innuitus* [= *M. oeconomus innuitus* Merriam], from St. Lawrence Island. GILMORE (1946, p. 40) placed *M. abbreviatus* in the subgenus *Stenocranius* and stated that it is a derivative of *M. miurus*. MILLER and KELLOGG (1955) and HALL and KELSON (1959) included *M. abbreviatus* in the subgenus *Stenocranius*, following NELSON and GILMORE.

ZIMMERMANN (1942) compared *M. abbreviatus* with *M. oeconomus*, concluding that the two are closely related but distinguishable at the specific level on the basis of differences in molar pattern. He considered the grouping of *M. abbreviatus* with *M. miurus* to be unnatural. RAUSCH (1953b) agreed with ZIMMERMANN's concept and later (1963) concluded that *M. abbreviatus* clearly belongs in the subgenus *Microtus*.

MATTHEY and ZIMMERMANN (1961), in a study of *M. middendorffi* Poliakov, noted (p. 66) that *M. middendorffi* does not appear to be closely related to any palaearctic species of *Microtus*, but that it shares certain characteristics with *M. abbreviatus* („Hüftdrüsen, extrem kurzer zweifarbiger Schwanz und Molaren-Muster vom *arvalis*-Typ.“). They observed further that, in contrast to members of the subgenus *Stenocranius*, the two species „... stimmen... in Körper-Maßen, Färbung, Haar-Struktur und Haar-Länge ebenso weitgehend überein wie in Schädelform und im Molaren-Muster.“ These authors remarked that their findings suggested a close relationship between the two species, noting that nothing contradicts the presumption that the cold-adapted *M. middendorffi* might have had a more extensive distribution during the Pleistocene, and that *M. abbreviatus* might represent a relict population of the former. They determined the karyotype for *M. middendorffi* but had no living specimens of *M. abbreviatus*. Until the affinities of *M. abbreviatus* could be deter-

mined by means of cytogenetic studies, they proposed that the two species be placed in a "*middendorffi*-group."

Cranial Characteristics of *M. abbreviatus*:

We compared *M. abbreviatus* with representatives of the subgenera *Microtus* and *Stenocranius*, utilizing for this purpose series of *M. oeconomus innuitus* Merriam (from St. Lawrence Island) and *M. gregalis muriei* Nelson (from the Brooks Range). *M. o. innuitus*, perhaps the largest form of *M. oeconomus*, exceeds *M. abbreviatus* in size; *M. g. muriei* is the largest representative of the species in North America.

Lacking a sufficient number of skulls from old adults, we included some of younger animals, but the respective series in composition were similar. As indicated by condylobasal length, minimum size of skulls in these series was: *M. abbreviatus*, 25 mm; *M. oeconomus*, 26 mm; *M. gregalis*, 24 mm. The resulting cranial measurements are summarized in Table 4. Unless otherwise stated, the comparisons below, however, were based on adult specimens.

The size and relative dimensions of the skull place *M. abbreviatus* in an intermediate position in relation to *M. gregalis muriei* and *M. oeconomus innuitus* (Fig. 18). Having a broader, more rounded brain case and a relatively greater zygomatic width

Table 4

Comparative cranial measurements for *M. gregalis*, *M. abbreviatus*, and *M. oeconomus* in millimeters

Species	Sex	No.	Condylobasal Length				Zygomatic Width			
			Range	\bar{M}	σ	SE \bar{M}	Range	\bar{M}	σ	SE \bar{M}
<i>gregalis</i>	♂	38	24.1—29.6	26.5	1.31	.212	10.8—16.1	13.0	1.15	.187
	♀	26	24.3—28.2	26.0	1.07	.211	11.2—14.3	12.6	.86	.170
<i>abbreviatus</i>	♂	33	25.3—31.7	28.1	1.11	.193	13.9—18.9	15.0	.92	.161
	♀	36	26.1—31.7	28.6	1.65	.275	13.3—18.8	15.6	1.65	.275
<i>oeconomus</i>	♂	31	26.0—32.8	30.2	1.90	.342	13.9—19.0	17.4	1.48	.266
	♀	33	26.0—30.8	28.9	1.39	.242	14.7—18.5	16.7	1.14	.202

Species	Sex	No.	Lambdoidal Width				Length Nasals			
			Range	\bar{M}	σ	SE \bar{M}	Range	\bar{M}	σ	SE \bar{M}
<i>gregalis</i>	♂	38	10.3—12.6	11.4	.53	.086	5.6—8.1	6.8	.65	.011
	♀	26	10.4—12.2	11.1	.44	.045	5.9—7.5	6.7	.41	.081
<i>abbreviatus</i>	♂	33	11.7—15.0	12.6	.59	.103	7.1—9.7	8.0	.51	.091
	♀	36	11.7—14.0	12.6	.60	.100	7.1—9.9	8.3	.74	.123
<i>oeconomus</i>	♂	31	12.1—15.1	13.8	.28	.051	6.9—9.5	8.6	.71	.128
	♀	33	12.1—14.5	13.2	.60	.105	7.0—9.0	8.2	.56	.098

Species	Sex	No.	Length Maxillary Tooth Row				Interorbital Width			
			Range	\bar{M}	σ	SE \bar{M}	Range	\bar{M}	σ	SE \bar{M}
<i>gregalis</i>	♂	38	5.6—6.7	6.1	.27	.043	2.8—3.6	3.2	.21	.035
	♀	26	5.4—6.6	6.0	.27	.054	2.9—3.6	3.2	.17	.034
<i>abbreviatus</i>	♂	33	5.8—7.5	6.5	.33	.058	3.6—4.0	3.7	.10	.018
	♀	36	5.9—7.5	6.6	.36	.061	3.5—4.3	3.8	.16	.027
<i>oeconomus</i>	♂	31	6.2—7.8	7.1	.41	.074	3.8—4.4	4.1	.15	.027
	♀	33	6.2—7.7	7.0	.05	.009	3.7—4.3	4.0	.17	.030

than that of *M. gregalis*, the skull of *M. abbreviatus* in dorsal view appears to lack characteristics of *Stenocranius* as defined by KASHCHENKO (1901) (see RAUSCH, 1964). The nasal bones are relatively long in *M. abbreviatus* and are in the ratio of their length to condylobasal length the same as in *M. oeconomus*. Largely because the maxillary and jugal segments are relatively narrow, the zygomata of *M. abbreviatus* appear less massive than those of *M. oeconomus*; the squamosal part of the zygoma is directed more anteriorly in *M. abbreviatus*, but not to so great a degree as in *M. gregalis*. *M. abbreviatus* resembles the latter species in that the zygomata are more curved anteriorly, with maximum zygomatic width attained at a level farther anterior than in *M. oeconomus*; in addition, in *M. abbreviatus* and *M. gregalis* the zygomatic arches are situated farther forward relative to the anterior margin of the squamosals. In *M. abbreviatus*, the masseteric plate is larger and tends more toward the horizontal than is the case in *M. oeconomus*. The interorbital region in width is rather uniform in *M. gregalis*, whereas it widens anteriorly to a greater degree in *M. abbreviatus*. The interorbital crest is not so strongly defined in the latter as in *M. gregalis*, nor do the anterior portions of the frontals form such prominent supraorbital ridges as in *M. gregalis*. The posterior margin of the interparietal projects posteriorly in both *M. abbreviatus* and *M. gregalis*, causing a corresponding deflection in the lambdoidal crest; although subject to variation, both the posterior margin of the interparietal

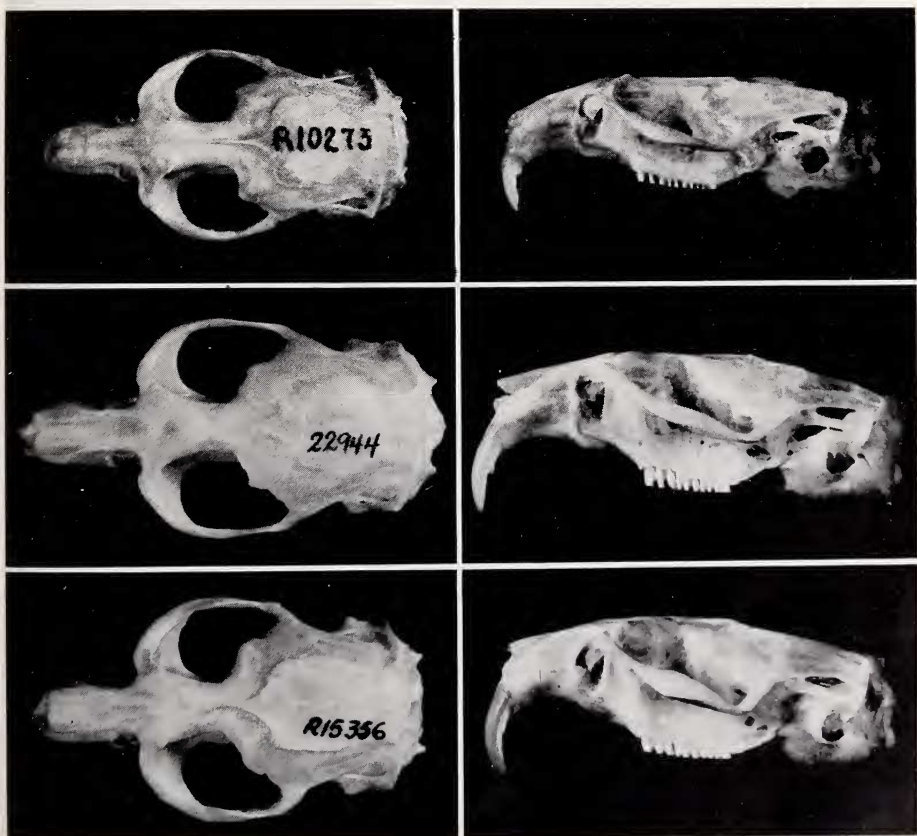


Fig. 18. Skulls (from top to bottom) of *M. gregalis*, *M. abbreviatus*, and *M. oeconomus*

and the lambdoidal crest are relatively straight in *M. oeconomus*. The dorsal margin of the supraoccipital is more or less straight in *M. abbreviatus*, whereas in the other two species it is definitely rounded.

The skulls of the three species differ as well in lateral view (Fig. 18). That of *M. gregalis* is relatively flat, the dorsal and ventral surfaces appearing in profile to be nearly parallel; the brain case of *gregalis* is little inflated, and the concavity in the interorbital region is emphasized by the strongly developed supraorbital crests. The relative length of the maxillary tooth row is similar in the three species, but the teeth of *M. gregalis* are smallest and most delicately formed. The incisors of *M. gregalis* also are relatively small, and their radius of curvature is least. The skull of *M. abbreviatus* is not so deep as that of *M. oeconomus*, but in ratio of depth of brain case to condylo-basal length, it approaches the latter more closely than does *gregalis*. The brain case of *M. abbreviatus* is more inflated than that of *M. gregalis*, and as in *M. oeconomus*, the dorsal surface of the skull is convex in profile. In lateral view, a difference is evident in the slope of the squamosal part of the zygoma in *M. abbreviatus* and *M. gregalis* as compared with *M. oeconomus*.

When the skulls are compared in ventral view, further similarities between *M. abbreviatus* and *M. gregalis* may be seen. Most obvious are the characteristic slope of the zygomata and the structure of the palate. In both species, when compared with *M. oeconomus*, the palate is relatively narrow and its surface is recessed dorsad between the alveolar rows. In transverse section, the palates of *M. abbreviatus* and *M. gregalis* are more U-shaped; that of *M. oeconomus* forms a relatively shallow arch. The teeth of *M. abbreviatus* are larger and heavier than those of *M. gregalis*, but the molar patterns are essentially identical. In *M. gregalis*, P_4 may have either five or six closed triangles, six preponderating in North American specimens (RAUSCH, 1964). In *M. abbreviatus*, the usual number, five, of closed triangles in P_4 demonstrate a lesser tendency for the separation of the secondary protoconulid to form a sixth. OSGOOD (1901, p. 65) noted that the upper incisors of *M. gregalis* are slightly sulcate on their anterior surfaces; this is true also for *M. abbreviatus*. The upper incisors of *M. oeconomus* lack sulci.

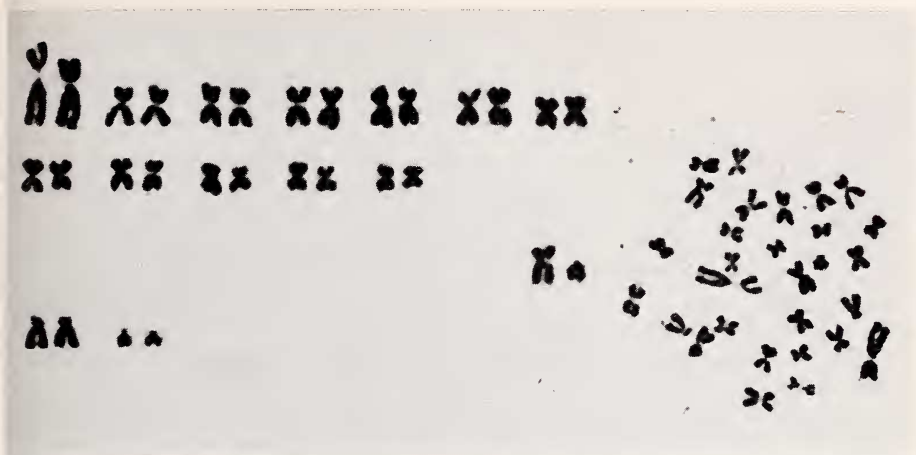
The immature skull of *M. abbreviatus* differs from that of *M. gregalis* in having a much more inflated brain case and a higher width/length ratio. Because of the similarity in form of the squamosal part of the zygoma, the zygomatic arches are nearly parallel in these species, whereas in the immature *M. oeconomus* the zygomata diverge posteriad.

The skull of *M. abbreviatus* was compared also with that of *M. middendorffi*. We agree with MATTHEY and ZIMMERMANN that *M. middendorffi* is a member of the subgenus *Microtus*. Cranially, it possesses none of the *Stenocranius*-like characteristics present in *M. abbreviatus*.

Chromosomes

Following the recommendation of MATTHEY and ZIMMERMANN (1961) that changes in taxonomic status of microtine rodents be supported by cytogenetic evidence, we prepared material for this purpose from bone marrow of both of the male voles captured in 1963 by F. H. FAY. The methods applied have been described elsewhere (RAUSCH, 1964). The karyogram of *M. abbreviatus* was compared with those of *M. gregalis* and *M. oeconomus* as well as with that of *M. middendorffi* published by MATTHEY and ZIMMERMANN.

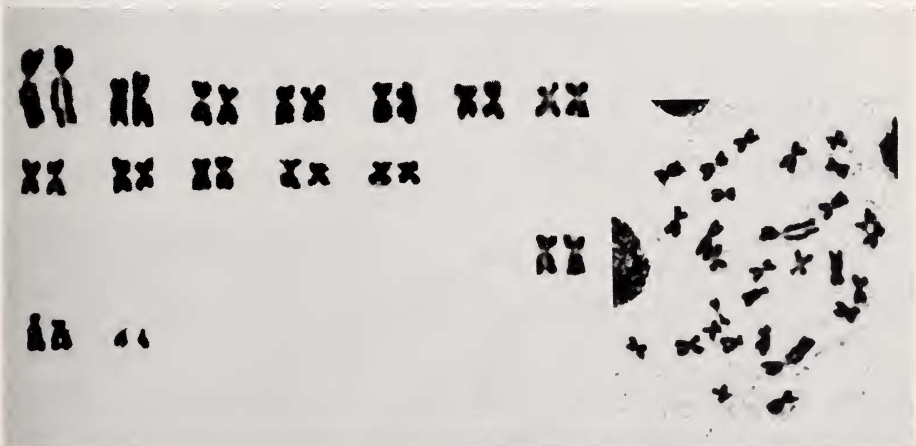
M. middendorffi. MATTHEY and ZIMMERMANN determined that *M. middendorffi* has a diploid number of 50 chromosomes. The heterochromosomes are metacentric and nearly homomorphous, and the fundamental number (N. F.) is 54. They considered

Fig. 19. Karyogram of *M. oeconomus*, male

this combination of characters to be unique among the species of *Microtus* for which karyograms have been defined.

M. oeconomus. The chromosomes of *M. ratticeps* [= *M. oeconomus uchidae* Kuroda, 1924] from Paramushir Island in the northern Kuriles have been investigated by MAKINO (1950), and the heterochromosomes of this species have been discussed by MATTHEY (1952). We utilized laboratory-reared specimens of *M. oeconomus operarius* Nelson, the stock of which originated in the southern part of the Kenai Peninsula, south-central Alaska. Although no specimens of *M. oeconomus immutus* were available, the karyogram of F_1 intergrades of these two subspecies was found to be identical with that of *M. oeconomus operarius*. Intergrades of the two are indefinitely fertile.

As did MAKINO in 1950, we determined the diploid number of chromosomes in *M. oeconomus* to be 30. Twelve pairs and the medium sized X-chromosome are metacentric or nearly so; one pair is submetacentric; and one pair of small chromosomes is acrocentric. The acrocentric Y-chromosome is larger than those comprising the acro-

Fig. 20. Karyogram of *M. oeconomus*, female

centric pair mentioned above. The fundamental number is 57 or 58. Karyograms of *M. oeconomus* are shown in Figs. 19 and 20. Our findings provide additional support for the generally accepted conclusion of ZIMMERMANN (1942) that *M. oeconomus* is a holarctic species.

M. gregalis. *M. gregalis muriei* has a diploid number of 54 chromosomes (RAUSCH, 1964). However, the karyogram published was determined from poor material, and identification of the heterochromosomes was uncertain. Further studies on voles of both sexes disclosed an error in the identification of the X-chromosome. Rather than being submetacentric and of medium size, as was indicated (RAUSCH, 1964, Fig. 7), the X-chromosome is large and metacentric. The Y-chromosome is very small and evidently submetacentric, with very short superior arms. Two pairs classified as submetacentric could possibly be considered as acrocentric. The fundamental number, therefore, may be either 71 (Y and 18 pairs acrocentric; 8 pairs submetacentric or metacentric), 72 (Y submetacentric), or 68 (sex chromosomes and 6 pairs metacentric or submetacentric, 20 pairs acrocentric). Karyograms of *M. gregalis* are shown in Figs. 21 and 22.

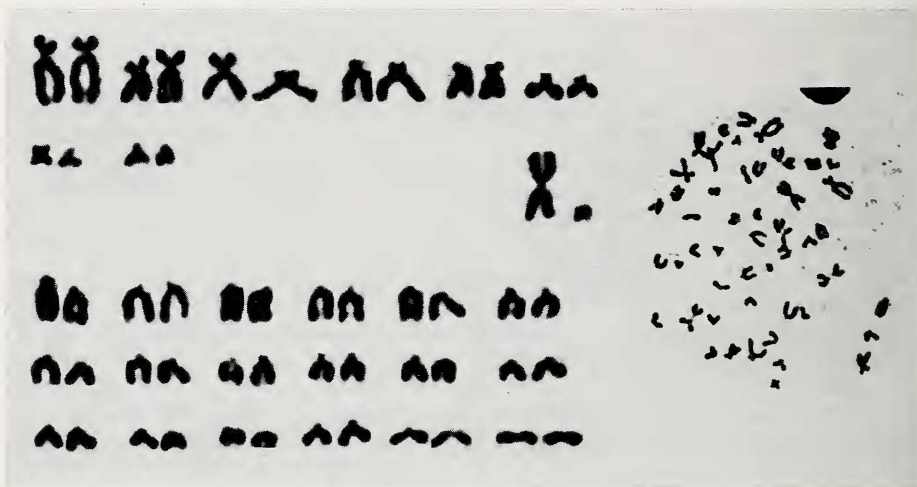


Fig. 21. Karyogram of *M. gregalis*, male

M. abbreviatus. A diploid number of 54 was determined for *M. abbreviatus*. The karyogram (Fig. 23) appears to be indistinguishable from that of *M. gregalis* as described above.

Hybridization

In an attempt to produce hybrids, a male *M. abbreviatus*, captured in July, 1963, was placed with a female *M. gregalis*. The latter, captured in October, 1962, had remained with a male *M. gregalis* for more than a year without producing young. The mixed pair was established on 10 November 1963. When the female died, on 9 December, two apparently full-term fetuses were present in the right uterine horn; apparent malposition of the lower individual probably was the cause of fatal dystocia. Since the gestation period of *M. gregalis* has never been found by us to exceed 21 days, we conclude that the fetuses were hybrids. Unsuccessful parturition is an occasional cause of maternal death in captive microtine rodents, and the dystocia in this case presumably was incidental.

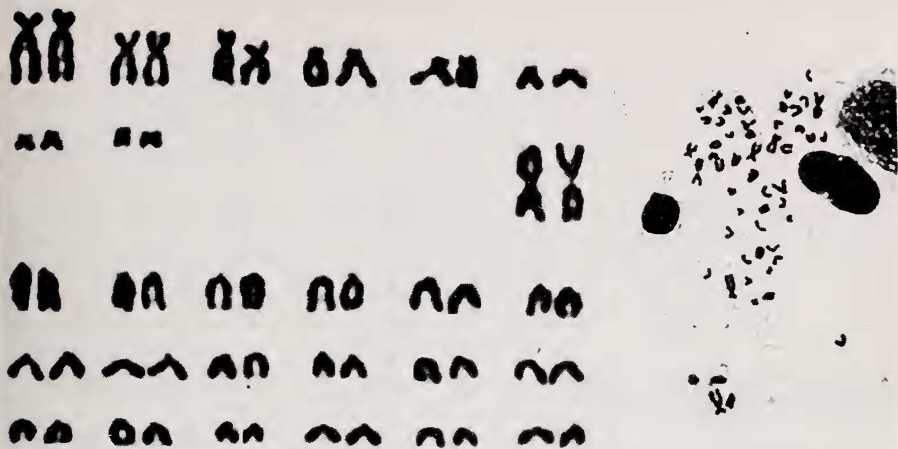


Fig. 22. Karyogram of *M. gregalis*, female

Discussion

M. abbreviatus possesses some cranial characteristics which ostensibly would place it in the subgenus *Microtus*, but others indicate an affinity with *M. gregalis*, the sole member of the subgenus *Stenocranius*. As shown by discrepant conclusions in the past concerning the systematic position of *M. abbreviatus*, its *Stenocranius*-like features are not strong. Only in retrospect, given the support of cytogenetic findings, does the significance of these features become apparent. OSGOOD (1901) was the first to

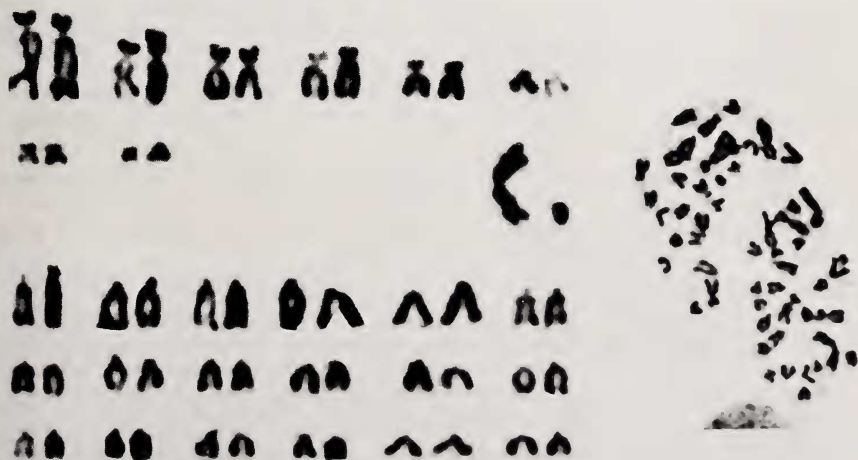


Fig. 23. Karyogram of *M. abbreviatus*, male

recognize that a close relationship exists between *M. abbreviatus* and *M. gregalis*. Consistent with his views and with those later expressed by GILMORE (1946), we conclude that *M. abbreviatus* is a geographically isolated derivative of *M. gregalis*.

The population of voles from which *M. abbreviatus* is derived must have been left on the highlands forming the St. Matthew Islands when the Bering-Chukchi platform (see Fig. 1) was inundated by a rise in sea level. This interpretation is compatible with the conclusions of HOPKINS (1959) that most of the Bering-Chukchi platform was exposed during the glacial maximum of Würm time, more than 35,000 years ago, when the level of the sea was about 100 m lower than it is at the present time. The extensive area so formed, comprising a major part of the unglaciated Amphiberingian Refugium, was covered again by the sea during a period of glacial recession about 35,000 to 25,000 years ago. As a result of glacial advances of late Würm time, about 25,000 to 12,000 years ago, lowering of sea level to about 60 m below that of the present again exposed much of the Bering-Chukchi platform. Excepting the few highlands, which remained as islands, the entire platform was finally inundated when the sea attained its present level between 11,000 and 10,000 years ago.

With a rise in sea level to about -36 m during the last interstadial, the highlands forming the St. Matthew Islands would have been widely separated from that part of the Bering-Chukchi platform remaining exposed (cf. HOPKINS, 1959). However, since these islands are bordered to the east by water ranging in maximum depth from about 59 to 66 m, a connection with the adjacent lowlands probably was re-established with the lowering of sea level to about -60 m during the last glacial phase of Würm time. Thus, a population of voles might have become isolated on these highlands more than 35,000 years ago, or the area might have been colonized during the last glacial phase, which ended about 12,000 years ago. That such small, comparatively delicate animals as voles could have colonized the islands other than by way of a land connection (i. e., via sea ice) is a possibility too remote to be considered further.

Other observations support the assumption that the voles on the St. Matthew Islands have been geographically isolated since the time of the penultimate glacial phase. *M. gregalis* seems to be adapted to life in comparatively dry alpine habitat; thus, the extensive lowlands which would have separated the peripheral highlands of the Bering-Chukchi platform from those to the north and east during the time of the last glacial phase might have been an effective ecological barrier. The comparatively high degree to which *M. abbreviatus* differs phenotypically from *M. gregalis* does not, however, constitute presumptive evidence of long geographic isolation.

The degree of phenotypic difference exhibited by the small mammals on other Bering Sea islands seems to be unrelated to the duration of isolation. The lemming on St. George Island (Pribilof group), for example, is little differentiated from that on the Alaskan mainland. Situated in deeper water near the edge of the Bering-Chukchi platform, St. George Island would have remained isolated by sea levels above -73 to -90 m, and therefore its population of lemmings must have become established before the end of the penultimate glacial phase of Würm time. This lemming, usually designated *Lemmus nigripes* True, 1894 (see HALL and KELSON, 1959), closely resembles *L. sibiricus* Kerr, 1792, which occurs on the Alaskan mainland. Besides a high degree of phenotypic similarity, these lemmings are cytogenetically similar, if not identical (both have $2N = 50$ chromosomes), and hybrids reared in the laboratory are indefinitely fertile. In contrast, St. Lawrence Island lies in relatively shallow water near the Eurasian mainland and clearly would have been a part of the exposed Bering-Chukchi platform during the last glacial phase (HOPKINS, 1959, Fig. 5). Of the three microtine rodents present on St. Lawrence Island, two (*M. oeconomus* and *Clethrionomys rutilus* Pallas) differ phenotypically from the mainland forms to a comparatively high degree. Hybrids between these and certain Alaskan mainland

subspecies are indefinitely fertile. Cytogenetic findings in *M. oeconomus* have been described above; those for *C. rutilus* will be reported elsewhere.

Although *M. abbreviatus* differs phenotypically from *M. gregalis*, genotypic differences are at most minor, and *M. abbreviatus* does not appear to be reproductively isolated. *M. abbreviatus* might be recognized as a well differentiated subspecies of *M. gregalis*. A final decision should await evaluation of the results of further cross-breeding experiments.

The comparatively slight differences existing between *M. a. abbreviatus*, on Hall Island, and *M. abbreviatus fisheri*, on St. Matthew, can be explained in that these islands are separated only by the shallow waters (ca. 18 m) of Sarichef Strait, by way of which an exchange of genes could have taken place at least as recently as late Würm time.

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Summary

The St. Matthew Islands, in the Bering Sea, have a flora and fauna comprised mainly of holarctic species. The terrestrial mammalian fauna included originally the polar bear, *Ursus maritimus* Phipps, the arctic fox, *Alopex lagopus* L., and an endemic vole, *Microtus abbreviatus* Miller. The polar bear has been exterminated by man, and reindeer were introduced on St. Matthew Island in 1944. Observations on the biology of *M. abbreviatus* on St. Matthew Island as well as in the laboratory are reported, including information on parasites and disease. Laboratory-reared animals were frequently affected by hyperplasia and papillomatosis of the gastric (squamous) epithelium, and well differentiated squamous-cell carcinoma was recognized in some cases. *M. abbreviatus* was compared morphologically and cytogenetically with *M. gregalis* Pallas and *M. oeconomus* Pallas, both of which occurred in the Amphiberingian Refugium during Würm time. Although *M. abbreviatus* possesses some cranial characteristics typical of the subgenus *Stenocranius*, phenotypically it differs rather strongly from *M. (Stenocranius) gregalis*. However, the two species have almost identical karyograms. The findings indicate that *M. abbreviatus* is derived from a population of *M. gregalis* isolated by eustatic rise in sea level, probably during the penultimate glacial phase of Würm time.

Zusammenfassung

Die Flora und Fauna der St.-Matthäus-Inseln im Bering Meer bestehen hauptsächlich aus holarktischen Arten. Ursprünglich bestand die Landsäugetier-Fauna aus drei Arten: Eisbär, *Ursus maritimus* Phipps, Polarfuchs, *Alopex lagopus* L., und einer endemischen Wühlmaus, *Microtus abbreviatus* Miller. Die Eisbären sind vom Menschen ausgerottet worden, und Herdenrene wurden 1944 nach St.-Matthäus-Insel eingeführt. Die Biologie der Wühlmaus auf St.-Matthäus-Insel und im Laboratorium, einschließlich Beobachtungen an Parasiten und Krankheiten, werden besprochen. In Zuchtieren wurden häufig papillomatöse Geschwülste des Magenepithels (Plattenepithel) gefunden, und Plattenepithelkarzinom wurde gelegentlich festgestellt. Die morphologischen und zytogenetischen Beziehungen zwischen *M. abbreviatus* und anderen Arten (*M. gregalis* Pallas und *M. oeconomus* Pallas), die während des Pleistozäns eine große Verbreitung in dem Amphibering'schen Refugium fanden, wurden untersucht. Auf Grund morphologischer (Schädel-)Merkmale steht *M. abbreviatus* zwischen den obengenannten Arten, die beziehungsweise den Untergattungen *Stenocranius* und *Microtus* angehören. Morphologische Schädelmerkmale verbinden *M. abbreviatus* mit der Untergattung *Stenocranius*, aber im Phenotyp unterscheidet sich *M. abbreviatus* erheblich von *M. (Stenocranius) gregalis*. Dagegen sind beider Karyogramme beinahe identisch. Man kann daher annehmen, daß *M. abbreviatus* aus einer Relikt-Population von *M. gregalis* stammt, die wahrscheinlich während der vorletzten Glazial-Phase auf den St.-Matthäus-Inseln isoliert wurde.

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